"Wosek-d1," strata that are now considered as U. Arenig or L. Llandeilo (Chazyan) in age. It has also been reported as occurring in strata of Upper Tremadoc and L. Arenig age in the Herault area of southern France. (Thoral, 1935, p. 162, pl. 13, figs. 4a, b, 5a, b).

It is clear, therefore, that the symmetrical *Babinka prima* type is the older. However, it seems quite unlikely that either the hinge types, nor the peculiar muscle patterns that mark "*Leda*" *bilunata* and "*Nucula*" *amica* could have been derived from those to be observed in *Babinka prima*. Two alternatives may be suggested: (1) that all three were derived from presently unknown pelecypod ancestors, or (2) that these early pelecypod types were polyphyletic in origin, and were separately derived from the prepelecypod ancestral stock. While it must be admitted that the known geologic occurrence of the species in question tempts one to place weight on the second possibility, it must be kept in mind that conditions of fossil preservation adequate for the observation of such details as the muscle scars are so rarely met with that it may well be that all three types of observed patterns represent offshoots from a common, and as yet unknown, stock.

In conclusion, therefore, it is the opinion of the writer that the muscle scars shown by these Ordovician pelecypods can be shown to be close to those exhibited by primitive gastropods, as figured by Knight; that they therefore may be interpreted as reflecting the musculature present in the ancestral stock from which the Pelecypoda were derived; and, in view of their similarity to the gastropod condition, that they afford evidence confirmatory to the arguments of Knight that the gastropods of the family Triblidiidae are close to the ancestral stock in the gastropod line. Further, they suggest that the adductor muscles of the Pelecypoda are derived from discreet pairs of the ancestral musculature, rather than from the union of multiple pairs.

BIBLIOGRAPHY

Barrande, Joachim. *Système Silurien de centre de la Boheme* **6**, Pelecypoda. Text and plates. 1881.

Knight, J. Brookes. *Paleozoic gastropod genotypes*. Geol. Soc. Amer. Spec. Pap. 32. 1941.

———. *Primitive fossil gastropods and their bearing on gastropod classification*. Smithsonian Misc. Coll. **117** (13). 1952.

Neumayr, M. *Beitrage zu einer morphologischen Eintheilung der Bivalven*. Denkschr. Akad. Wiss. Wien, Math-Nat. Kl. **58**: 701–801. 1891.

Pelseneer, Paul. *Mollusca*. *In* Lankester, E. R., "A Treatise on Zoology," pt. 5. 1906.

Pfab, Leo. *Revision der Taxodonta des B hmischen Silurs*. Palaeontographica **80**, Abt. A: 195–253. 1934.

Thoral, Marcel. *Contribution à l'étude paléontologique de l'Ordovician inférieur de la Montagne Noire et révision sommaire de la fauna cambriénne de la Montagne Noire*. Théses pres. Fac. Sci., Univ. Paris. Montpellier, 1935.

MYCOLOGY.—Aphanomyces euteiches *from pea roots and* "Aphanomyces euteiches *P. F. 2.*"

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The original account (Jones and Drechsler, 1925) of my *Aphanomyces euteiches* was based entirely on the saprolegniaceous parasite that occurs during wet seasons as a causal agent of serious root rot in garden peas (*Pisum sativum* L.). Soon after the account was published Linford (1927) reported having found oospores typical of the fungus also in diseased roots of narrow-leaved vetch (*Vicia angustifolia* L.) seedlings as well as in diseased seedlings of alfalfa (*Medicago sativa* L.) and sweet clover (*Melilotus alba* Desr.). He further observed several varieties of sweet peas (*Lathyrus odoratus* L.) greatly weakened from spontaneous attack by the parasite, and in inoculation trials successfully infected nine additional leguminous species. Mainly because of similarities shown by oospores found in their decaying roots he considered four nonleguminous plants including barley (*Hordeum vulgare* L.) and oats (*Avena sativa* L.) subject to invasion by *A. euteiches*. Subsequent study of a culture isolated by Linford from an oat root, however, revealed distinctive morphological and developmental features; wherefore it was used as type material of a separate species, *A.*

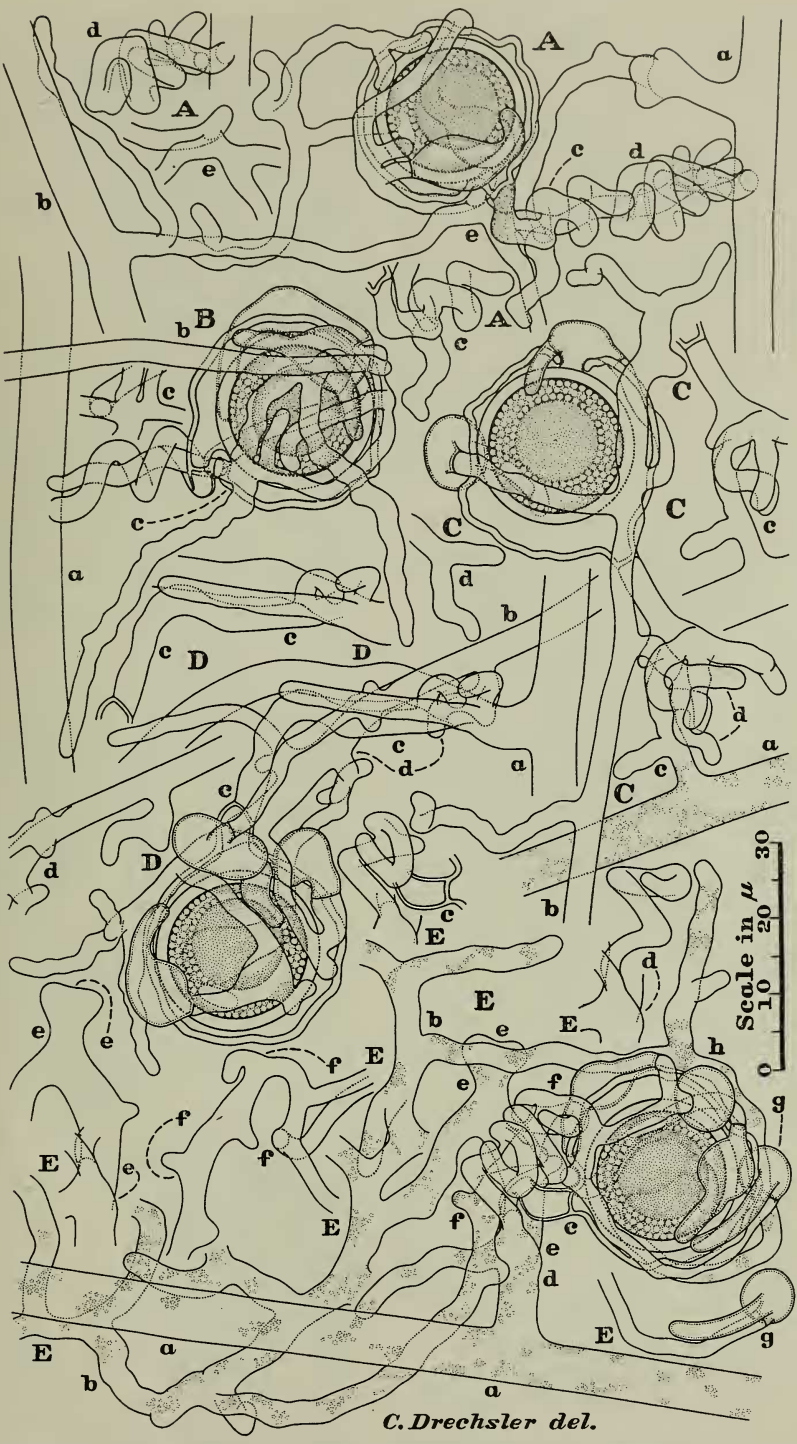

FIG. 1.—Mature sexual reproductive apparatus of the isolation received from the Centraalbureau voor Schimmelcultures at Baarn, Netherlands, as *Aphanomyces euteiches* P. F. 2; × 1,000 throughout. A–D, Diclinous reproductive units, with one mycelial hypha, a, supplying the oogonium, and another hypha, b, supplying the attendant antheridia. E, Reproductive unit with traceable mycelial connection between the stout mycelial filament, a, that supplies the oogonium and the hypha, b, that supplies the 5 attendant antheridia. For greater clearness some of the more complicated portions of the several units (A, c–e; B, c; C, c, d; D, c, d; E, c–h) are shown separately as well as in proper position.

camptostylus Drechsler (1929). Similarly a number of cultures isolated from tomato (*Lycopersicon esculentum* Mill.) roots in 1926, which at first had been referred (Drechsler, 1927) to *A. euteiches*, were on closer examination found to represent a different species that I then presented (Drechsler, 1929) under the binomial *A. cladogamus*. More recently Doran, Guba, and Gilgut (1942) in Massachusetts reported that *A. euteiches* often causes damping-off of celery (*Apium graveolens* L.). Detailed evidence concerning the relationship of *A. euteiches* to any *Aphanomyces* cultures that may perhaps have been isolated from celery or barley in the United States has not so far been supplied.

In the scanty relevant European literature a few nonleguminous plants are cited as hosts of *Aphanomyces euteiches* or are mentioned as having yielded cultures referable to that species. Buisman (1927, p. 45) in the Netherlands isolated from decaying roots of pansies (*Viola tricolor* var. *hortensis* Hort.) an *Aphanomyces* which to her looked very similar to *A. euteiches* but which in her inoculation experiments did not attack pea roots. She was unable to try it out on pansies and thus did not establish whether her fungus was the cause of an acute root rot which she mentioned as appearing in her experimental garden. In cross-inoculation experiments later carried out by Meurs (1928) an isolation of *A. euteiches* was found capable of infecting peas, but incapable of infecting either *Viola tricolor* or *V. cornuta* L.; whereas the pansy-root *Aphanomyces* was found incapable of infecting peas, but capable of infecting both *V. tricolor* and *V. cornuta*. Meurs, like Buisman, held the pansy fungus to be morphologically identical with the parasite causing pea root rot, though he recognized that it presented some differences in growth as well as in parasitism. He therefore considered it a physiological form of the same species, and designated it as *A. euteiches* P. F. 2. Further he concluded that it was the cause of an acute root rot of pansies in Holland. It seems noteworthy that Meurs came to this conclusion even though he had obtained from the pansy other fungi that might have been regarded as likely root parasites. Of nine cultures he isolated from *Viola tricolor* he assigned two to *Pythium intermedium* DeBary and four to *P. irregulare* Buisman, and listed two as belonging to undetermined species. Besides *V. tricolor* he listed two other plants, *Spinacia oleracea* L. and *Arabis alpina* L., as having each yielded a culture of *Aphanomyces euteiches* P. F. 2.

A decade later Van Eek (1938) reinvestigated pansy root rot in the Netherlands with results strongly divergent from those of Meurs. In repeating the tests described by Meurs and employing the same strain of "*Aphanomyces euteiches* P. F. 2," Van Eek obtained only slight evidence of pathogenicity. He concluded accordingly that *A. euteiches* P. F. 2 could not be the causal agent of severe root rot of pansies. In view of the possibility that the original strain of "*A. euteiches* P. F. 2" might have lost its virulence during the years it had been kept in culture Van Eek reisolated the strain from a successfully infected plant, but the recovered isolation likewise showed only meager aggressiveness. Apparently he obtained no new culture that was referable to *Aphanomyces*. However, despite the general infrequence of saprolegniaceous fungi as plant pathogens he isolated two such fungi —his *Brevilegnia gracilis* and his *B. macrospora*—from diseased pansy plants and found both to be strongly parasitic.

Soon after Meurs had designated as *Aphanomyces euteiches* P. F. 2 the water mold he and Buisman had isolated from pansies a culture contributed by him under that designation was supplied to me from the Centraalbureau voor Schimmelcultures at Baarn, Netherlands. In observance of precautions advisable with organisms of foreign origin the culture was never used in inoculation trials of any kind either outdoors or in the greenhouse. However, it was compared side by side on several different agar substrata with *A. euteiches* from pea roots, with several congeneric isolations obtained from pansies in and near the District of Columbia (Drechsler, 1934), and with the strains of *A. cladogamus* obtained from roots of flax (*Linum usitatissimmum* L.) and spinach (*Spinacia oleracea* L.) in the United States (Drechsler, 1935). The

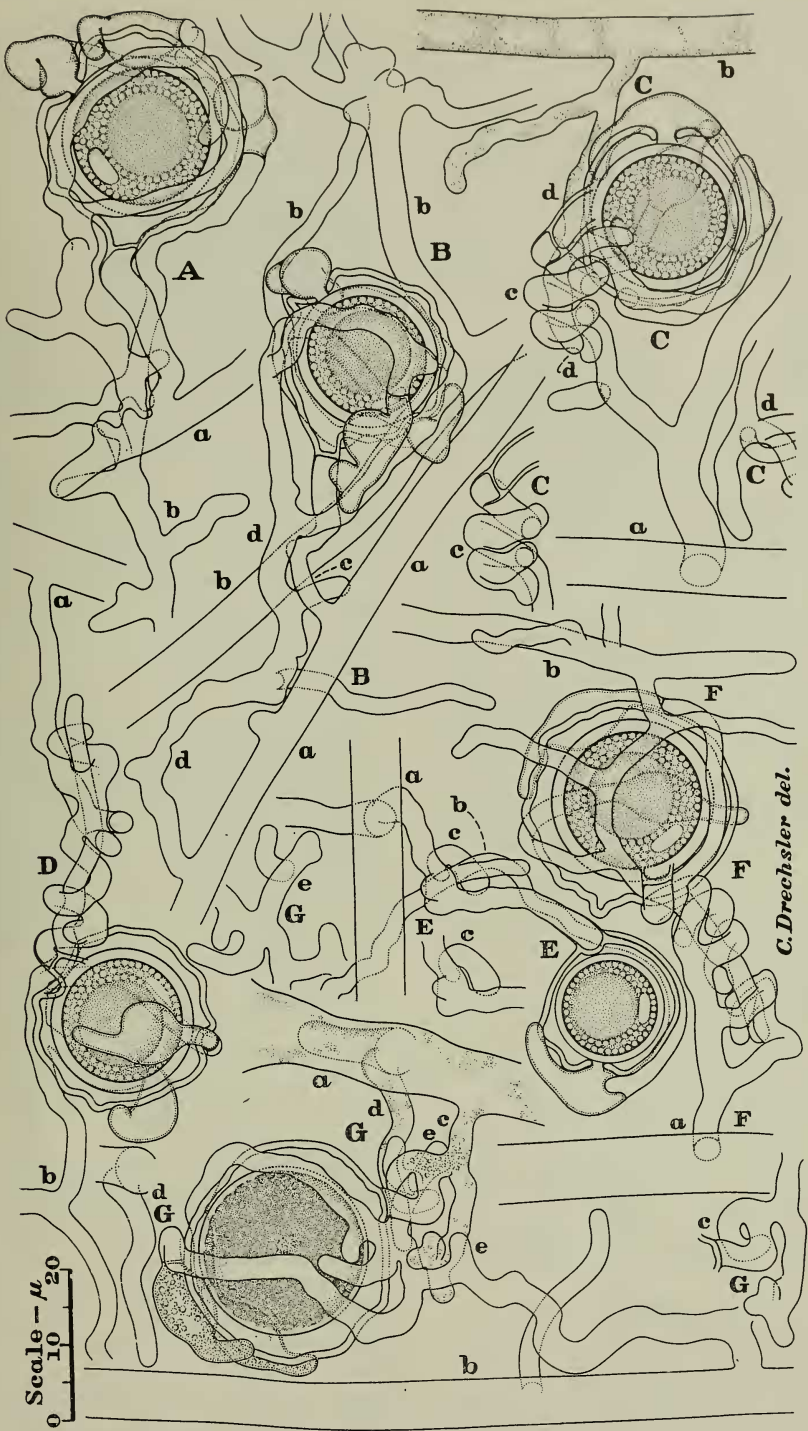

FIG. 2.—Sexual reproductive apparatus of the isolation received as *Aphanomyces euteiches* P. F. 2; × 1,000 throughout. A–G, Diclinous reproductive units, with one mycelial hypha, a, supplying the oogonium, and another hypha, b, supplying one (B, E) or more (A, C, D, F, G) attendant antheridia; in B two antheridia of monoclinous origin (upper left, lower middle) are present besides, these being supplied from a branch, d, that is given off by the same hypha as the oogonial stalk, c. Oospore in early stage of development in G, but fully mature in A–F. For greater clearness some of the more complicated parts in three of the units (C, c, d; E, c; G, c–e) are shown separately as well as in proper position.

Dutch isolation displayed generally greater intricacy in the make-up of its sexual reproductive apparatus than any of the isolations with which it was compared. Despite the rather complicated appearance of the 15 reproductive units figured herein (Fig. 1, A–E; Fig. 2, A–G; Fig. 3, A–C) to show the postural and positional relations of the sex organs, these units hardly reveal the full scope of complexity displayed by the fungus.

With respect to the hyphal connection of its sex organs the culture designated as *Aphanomyces euteiches* P. F. 2 resembled *A. cladogamus* more closely than *A. euteiches*. While in many of its reproductive units the hypha (Fig. 1, A–D:a; Fig. 2, A–G:a) bearing the oogonial stalk showed no visible connection with the hypha (Fig. 1, A–D:b; Fig. 2, A–G:b) supplying an antheridial branch, it commonly gave rise here and there to monoclinous or androgynous units in which a connection between the female branch (Fig. 3, A–C:a) and the male branch (Fig. 3, A–C:b) could be traced readily. In more complicated units it was often difficult to follow even a fairly short mycelial connection (Fig. 1, E, d, e) between an oogonial stalk (Fig. 1, E, c) and the wide axial filament (Fig. 1, E, a) from which it was supplied, or to make out an existing connection between the oogonial stalk (Fig. 1, E, c) and the hypha (Fig. 1, E, b) from which was given off the branch or branches (Fig. 1, E, f, h) supplying one or more attendant antheridia (Fig. 1, E, g). Occasionally a branch (Fig. 2, B, d) given off by the same mycelial hypha (Fig. 2, B, a) as the oogonial stalk (Fig. 2, B, c) was found to supply one or more attendant antheridia (Fig. 2, B, upper left, lower middle) apart from any antheridia (Fig. 2, B, lower right) supplied from a neighboring hypha (Fig. 2, B, b).

The complicated make-up frequent in sexual reproductive apparatus of "*Aphanomyces euteiches* P. F. 2" came about in large measure from entwinement of hyphal parts. Sometimes the oogonial stalk entwined a ramification of the antheridial branch (Fig. 1, B). Sometimes an antheridial branch (Fig. 1, E, f) or the terminal portion of a hypha bearing one or more antheridial branches (Fig. 2, C, D, F) was entwined not only by the oogonial stalk but also by short ramifications borne on it. Often, again, a prolongation of a hypha (Fig. 1, A, e) bearing antheridial branches was entwined by a branch (Fig. 1, A, c) given off from the oogonial stalk, or even by a branch (Fig. 1, A, d) from the mycelial filament (Fig. 1, A, a) bearing the oogonial stalk. Reproductive units with little of no intertwining of hyphal parts acquired in many instances an intricate appearance through interlocking of spurs extended from the branches bearing the apposed sex organs (Fig. 1, C, c, d: Fig. 2, E, c).

Two hundred oogonia of "*Aphanomyces euteiches* P. F. 2" taken at random in maize-meal agar plate cultures 30 days old gave measurements for diameter, expressed in the nearest integral number of microns, with the following distribution: 18μ, 1; 20μ, 5; 21μ, 6; 22μ, 16; 23μ, 18; 24μ, 33; 25μ, 40; 26μ, 35; 27μ, 19; 28μ, 13; 29μ, 6; 30μ, 3; 31μ, 3; 32μ, 1; 33μ, 1. The 200 oospores of correct internal organization within these oogonia gave measurements for diameter distributed thus: 16μ, 4; 17μ, 13; 18μ, 26; 19μ, 38; 20μ, 47; 21μ, 38; 22μ, 20; 23μ, 11; 24μ, 3. Averages of 25.0μ and 19.8μ were computed for oogonial diameter and oospore diameter, respectively. In the 200 reproductive units the oogonial envelope varied from .5 to 1.3μ in thickness, averaging .8μ in this dimension; while the oospore wall measured 1 to 1.9μ in thickness and averaged 1.5μ. Measurements for diameter of the reserve globule in the individual oospores ranged from 9 to 16μ, and gave an average of 11.4μ.

Thus in its main dimensions the culture isolated in the Netherlands would not seem to have differed markedly from *Aphanomyces cladogamus*. Owing to the difficulty of ascertaining from a single culture the importance of hyphal entwinement attendant to sexual reproduction it appears about equally uncertain whether "*A. euteiches* P. F. 2" should be included in *A. cladogamus* or should be kept separate from that species. Study of additional cultures from pansies in the Netherlands may be necessary before a sound decision can be reached as to the proper disposition

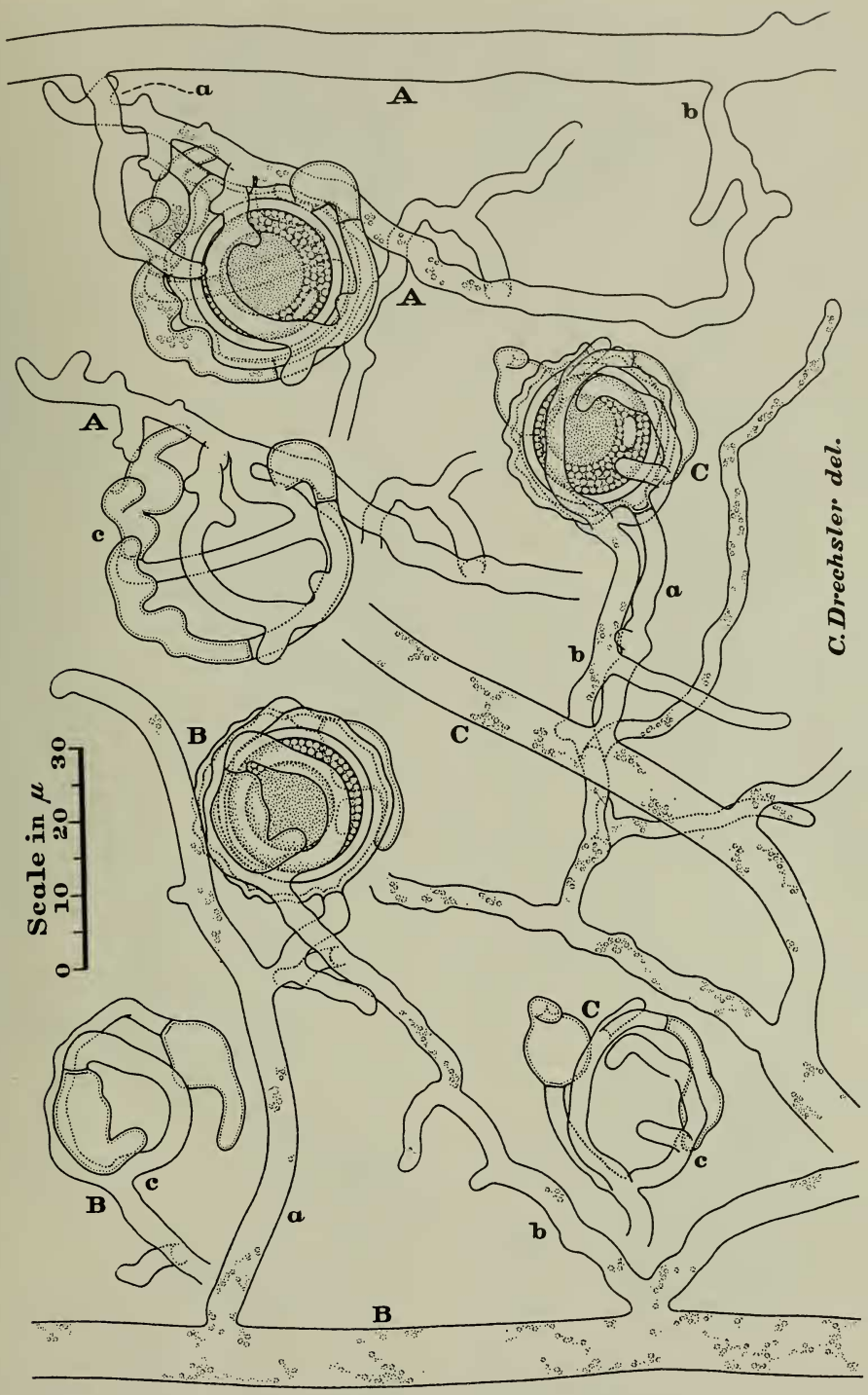

FIG. 3.—Mature sexual reproductive apparatus of the isolation received from the Centraalbureau voor Schimmelcultures at Baarn, Netherlands, as *Aphanomyces euteiches* P. F. 2; all reproductive units formed in maize-meal agar plate cultures, and drawn at a uniform magnification with the aid of a camera lucida; × 1,000 throughout. A–C, Monoclinous reproductive units, showing mycelial connection between the hyphal branch, a, supplying the oogonium and the hyphal branch, b, supplying the attendant antheridia; for greater cleanness the entire male complement of each unit is shown besides in a separate drawing, c.

of the fungus dealt with by Buisman and by Meurs.

Whatever its relation to *Aphanomyces cladogamus* the fungus received as *A. euteiches* P. F. 2 was assuredly not to be held conspecific with *A. euteiches* occurring in pea roots. Its oogonial envelope, being relatively thin and pliable, would usually shrink more or less irregularly after the oospore had been formed, and consequently in mature reproductive apparatus most often showed a somewhat undulating profile. In true *A. euteiches*, on the other hand, the oogonial envelope is conspicuously thicker (Fig. 4, A–F). After formation of the oospore it behaves more nearly like a rigid shell, and in agar culture usually maintains its smoothly spherical outer contour for many weeks without evident change in size and shape.

Pronounced helicoid intertwinement of hyphal parts is not characteristic of sexual reproduction in *Aphanomyces euteiches* from pea roots. In maize-meal agar plate cultures of the pea-root parasite the mycelial connection between an oogonium and its attendant antheridia is generally too remote to be traced. Sometimes, however, the oogonium of one reproductive unit (Fig. 4, A, a) and the male complement of a neighboring reproductive unit (Fig. 4, A, b) are found supplied by the same mycelial filament (Fig. 4, A, c) from positions perhaps less than 50μ apart; the other sex organs of the two units being then usually contributed by two separate mycelial filaments (Fig. 4, A, d, e). Most often one hypha gives rise to the oogonium either distally (Fig. 4, B, a) or on a short lateral stalk (Fig. 4, C, a; D, a; E, a), while another hypha near by (Fig. 4, B, b; C, b; D, b; E, b) gives off the antheridial branch or branches that bear terminally all the attendant male cells. Rather commonly the oogonial stalk and antheridial branch appear in some measure interlocked by means of lateral spurs. In instances where an oogonium is supplied with antheridia from 2 or 3 mycelial hyphae (Fig. 4, F, b, c, d) only one of these hyphae (Fig. 4, F, b) is usually found interlocked with the mycelial filament (Fig. 4, F, a) giving off the oogonial stalk.

Aphanomyces euteiches was listed by Dennis and Foister (1942) as the cause of a root rot of *Viola* spp. (including the pansy and violet) observed by them in 5 regions comprising the central and eastern sections of Scotland. A typewritten circular (Anonymous, 1931) issued earlier from the Royal Botanic Garden in Edinburgh stated that Violas grown on the same land for a number of years often contract a disease from which the stem turns brown and shrivels, and the leaves turn yellow; death of the individual plants ensuing after the stem has decayed for an inch or two. On microscopical examination of the stem, collar, and decaying root numerous spherical bodies with slightly thickened walls were observable, being found mainly in the vascular elements. These bodies were identified as oospores of the causal agent of the root rot, a species of *Aphanomyces* similar to *A. euteiches*. Yet no species of *Aphanomyces* is mentioned by Chesters and Hickman (1939, 1944) in either of the 2 papers setting forth some fungus parasites they observed through examination of numerous varieties of *Viola* and pansy received from all parts of Britain and found affected with a soft rot of the stem or of the root system. In the final stages of the disease complex discussed by Chesters and Hickman, much as in the disease described in the Edinburgh circular, the leaves wilt and shrivel, and the whole plant collapses.

The occurrence of *Aphanomyces* oospores in the woody cylinder—a feature noted also in the roots of severely diseased pansies in and near the District of Columbia—suggests that the *Aphanomyces* attacking cultivated violets and pansies in Scotland may be identical with the species that attacks pansies in the United States rather than with the species that causes root rot in peas.

REFERENCES

Anonymous. *Root-rot of Violas caused by a species of* Aphanomyces: 2 pp. (typewritten). Royal Botanic Garden, Edinburgh, 1931.

Buisman, C. J. *Root rots caused by phycomycetes.* Meded. Phytopath. Labor. Willie Commelin Scholten **11**: 1–51. 1927.

Chesters, C. G. C., and Hickman, C. J. *Preliminary report on stem and root rot of* Viola and *pansy.* (Reprint from) Nat. Viola and Pansy Soc. Yearbook 1938: 1–8. 1939.

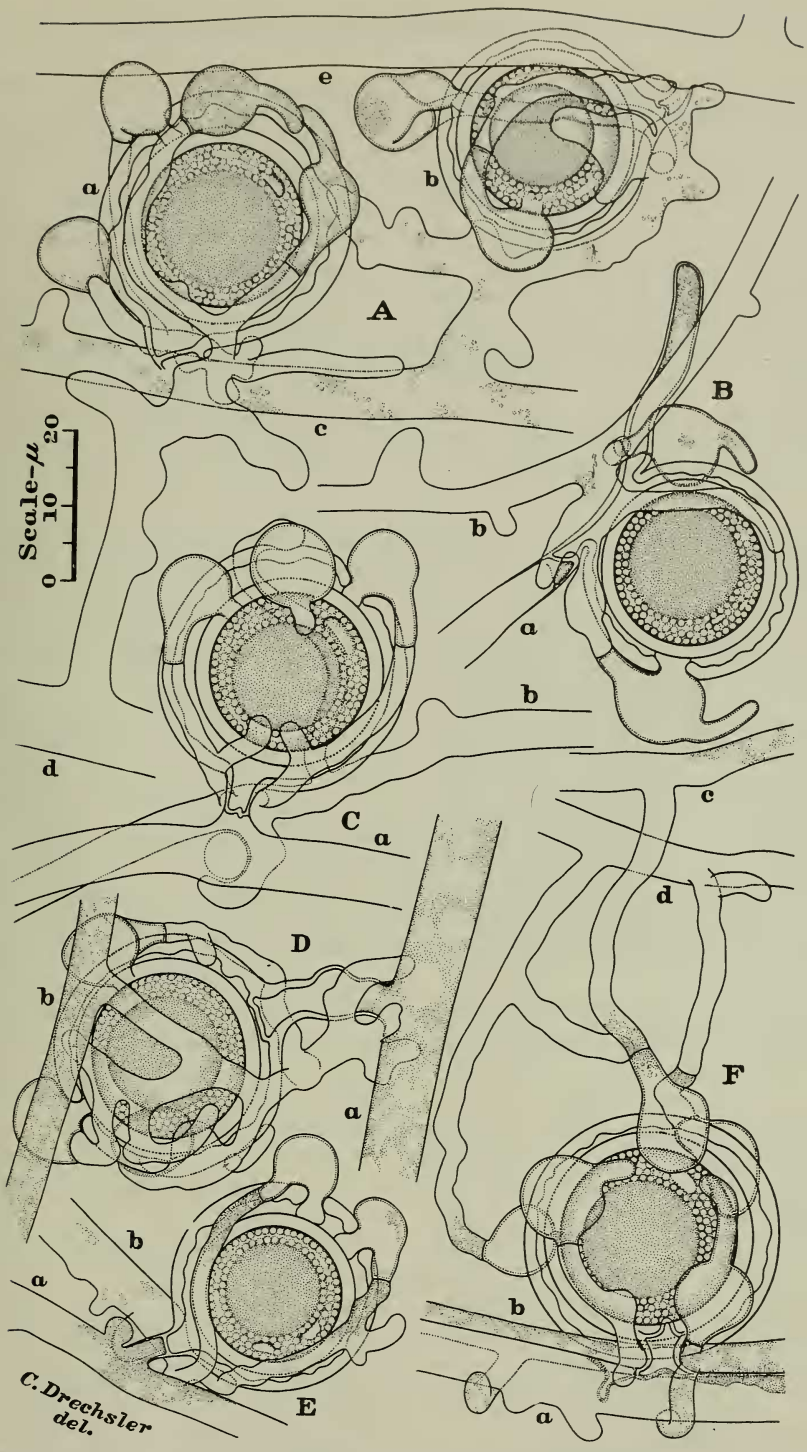

FIG. 4.—Mature sexual reproductive apparatus of the pea root-rot parasite, *Aphanomyces euteiches*; all reproductive units formed on the under side of maize-meal agar plate cultures; × 1,000 throughout. A, Two connected reproductive units, a and b; c, mycelial hypha supplying the oogonium of unit a and the antheridia of unit b; d, mycelial hypha supplying antheridia of unit a; e, mycelial hypha supplying oogonium of unit b. B–E, Diclinous reproductive units, each showing origin of oogonium from one mycelial hypha, a, and origin of attendant antheridia from a neighboring hypha, b. F, Diclinous reproductive unit showing oogonium supplied by one mycelial hypha, a, and its male complement of 5 antheridia supplied conjointly by 3 neighboring hyphae, b–d.

———. *On* Pythium violae *n. sp. and* P. oligandrum *Drechsler from cultivated* Viola. Trans. Brit. Mycol. Soc. **27:** 55–62. 1944.

Dennis, R. W. G., and Foister, C. E. *List of diseases of economic plants recorded in Scotland.* Trans. Brit. Mycol. Soc. **25:** 266–306. 1942.

Doran, W. L., Guba, E. F., and Gilgut, C. J. *The control of damping-off of vegetables by formaldehyde and other chemicals.* Massachusetts Agr. Exp. Stat. Bull. 394: 20 pp. 1942.

Drechsler, C. *Two water molds causing tomato rootlet injury.* Journ. Agr. Res. **34:** 287–296. 1927.

———. *The beet water mold and several related root parasites.* Journ. Agr. Res. **38:** 309–361. 1929.

———. *Vascular wilt and root rot of pansies due to* Aphanomyces *sp.* (Abstract) Phytopathology **24:** 7–8. 1934.

———. *Occurrence of a species of* Aphanomyces *on roots of spinach and flax.* (Abstract) Phytopathology **25:** 14–15. 1935.

Jones, F. R., and Drechsler, C. *Root rot of peas in the United States caused by* Aphanomyces euteiches (*n. sp.*). Journ. Agr. Res. **30:** 293–325. 1925.

Linford, M. B. *Additional hosts of* Aphanomyces euteiches, *the pea rootrot fungus.* Phytopathology **17:** 133–134. 1927.

Meurs, A. *Wortelrot, veroorzaakt door schimmels uit de geslachten* Pythium *Pringsheim en* Aphanomyces *De Bary:* 95 pp. Baarn, 1928.

Van Eek, T. *Root-rot of* Viola tricolor maxima *Hort.* Phytopath. Zeitschr. **11:** 217–281. 1938.

ZOOLOGY.—*Observations on the feeding of prostigmatid larvae (Acarina: Trombidiformes) on arthropods.*[1] G. W. Wharton, University of Maryland.

In 1892 M. S. Jourdain, speaking to the Parisienne Academy of Science, described two methods by which larval prostigmatid mites obtain their food from the arthropods which they parasitize. One method consisted simply of the mite piercing the thin integument between the sclerites in order to withdraw blood. The second method involved the formation of a branched feeding tube or stylostome in addition to the puncture. In 1899 Jourdain figured such a tube produced by *Trombidium holosericieum* in its host.

André in 1930 reviewed the observations of earlier workers on the branched stylostomes of trombidiid larvae and called attention to the work of Flögel, 1876, as well as to that of Jourdain. André compared these stylostomes to those produced by *Trombicula autumnalis* in vertebrates and concluded that the stylostomes of parasites of vertebrates and invertebrates are formed by secretions of the larvae. The branching of the stylostomes of certain of the parasites of invertebrates he ascribed to a postulated system of lacunae in the subdermal tissues of the host through which the secretions of the larvae are channeled.

Marshall and Staley in 1929 reported and figured unbranched stylostomes in mosquitoe larvae produced by larvae of water mites that were thought to be similar to *Lebertia tauinsignata.* They recognized that the stylostomes were subdermal but they considered them to be made of chitin and to be products of the host. Feng and Hoeppli (1933) reviewed the entire problem and studied sections of feeding tubes in parasitized mosquitoes. Host cells were shown to be involved in the formation of these tubes, and they support the conclusion of Marshall and Staley. Recently Jones (1950) has discussed the earlier works with reference to the formation of the feeding tube in vertebrates. He recognized that the stylostome was made up of a narrow central canal surrounded by a hyaline mass. The hyaline mass is said to be formed from keratinized malpighian cells.

In the course of investigations on the feeding mechanisms of pest chiggers, *Trombicula alfreddugèsi* and others, a number of prostigmatid larval parasites of arthropods was examined, but only *Trombidium* sp. on the common firefly *Photuris pennsylvanica* formed a stylostome. The multiple branching of the stylostome was readily observed in whole mounts of dissections (Fig. 1), and the nature of the wound could be seen in serial sections. The larvae attached themselves to the synarthrodial membranes between the anterior abdominal sclerites beneath the elytra. The larvae were invariably aligned with the long axis of the host with their anterior ends directed

[1] This work was supported by a grant from the National Institutes of Health, U. S. Public Health Service, to Duke University.